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THE CONTINUITY OF DEVELOPMENT

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CONTINUITY of development in a broad sense hardly calls for discussion here. The paleontologic evidence in its favor is so extensive and so universal that the perfection of the proof is merely a question of the completeness of the evidence. The question for discussion is rather as to the method of race development and specific change—whether continuous, by the slow accumulation of minute individual variations, definite or indefinite, through the influence of natural selection or of other causes—or discontinuous by the sudden appearance of distinct mutations or sports, usually of subspecific or specific value, sometimes of generic value. This question is much debated nowadays, and it would seem that the evidence from paleontology ought to be of the first importance in deciding it.

It is very commonly asserted that this evidence is strongly in favor of discontinuous development. This would mean that new species and even genera appear, as a rule, suddenly at certain levels, and that the record of a phylum is not usually a slow continuous change from one species into another as we pass upward from stratum to stratum; but that one species has a certain vertical range and is then supplanted by another species, this in turn by a third, and so on, each successive stage being an advance over the preceding, but the species overlapping instead of grading.

I think that there is no question but that in vertebrate paleontology the evidence taken at its face value does appear to be very distinctly in favor of discontinuous development. Where we are able to follow a phylum of Tertiary mammalia through a series of strata in one locality, we find that the successive stages appear, as a rule, full formed at certain levels, supplant and replace the more primitive stages, and are in turn supplanted and replaced by more advanced stages. In former years, when the records of locality and level were less exact, it was possible to arrange a series of gradations from one stage to another among the specimens pertaining to a particular phylum, and to assume that this gradation corresponded to the levels in the formation at which the specimens had been collected, and that the specific change was through continuous gradation. The more exact records of locality and level and the more extensive and complete collections in recent years have in general failed to confirm this arrangement. In the great majority of cases, so far as the record shows, new species appear already

distinct, at first sporadically along with the more primitive ones, then more abundantly, finally replacing the older ones altogether. The intermediate gradations occur along with the more typical individuals, but without much definite relationship to intergradation in the succession of strata.¹

We may illustrate from the evolution of the oreodonts, as these are the most abundant and most completely known of American fossil mammals.

The earliest known representatives of the phylum are *Protoreodon* and *Protagriochærus* from the Upper Eocene Uinta beds of Utah. Both have very short crowned teeth with five crescents on the upper molar, the fifth crescent quite distinct. The fourth premolar is not molariform. For the next stage we have to shift to another formation, 400 miles away, the White River. In the lowest strata of this formation, the Titanotherium beds, we find *Oreodon*, *Bathygenys* and *Agriochærus*, all with decidedly longer crowned teeth, and no trace of the fifth crescent in the molars. In *Oreodon* and *Bathygenys* the fourth premolar is non-molariform, composed of one inner and one outer crescent, as usual among Artiodactyls. In *Agriochærus* it has become imperfectly molariform with two outer crescents and one inner one. Between the Uinta and White River oreodonts a sharp break intervenes and no intermediates are known. From this point we can trace the subphyla of oreodonts up through a considerable succession in the Big Badlands of South Dakota and the adjoining region. *Oreodon culbertsoni*, *O. bullatus*, *Eucretaphus*, *Eporeodon*, *Mesoreodon* and *Merychyus* appear to be approximately successive stages in specialization. The skull is shortened, the teeth become longer crowned, the tympanic bullæ are enlarged, lachrymal vacuities appear, the limbs are lengthened, the feet lengthened and compacted and the thumb is lost. But there is not a continuous intergradation in any of these features as we pass upward in the beds. Oreodonts with small bullæ are abundant in the lower and middle White River, the bullæ varying very little in size. A species with medium-sized bullæ occurs occasionally associated with them. In the Upper White River all the oreodonts that I have seen have bullæ of large size. The size of the bulla, then, does not increase continuously as we go up through the formation. Another and much more specialized genus of oreodonts, *Leptauchenia*, suddenly appears in abundance in the Upper White River. I have seen a single specimen of this genus from the Middle beds, but it shows no more primitive features than those of the Upper beds. In the Lower Rosebud, immediately overlying the White River, species of *Eporeodon* are common, like

¹ The statements of fact herein contained are based partly upon field experience, chiefly upon the records of some 20,000 specimens of fossil mammals and reptiles in the American Museum collections, most of which the writer has had occasion to examine and identify and to post the field records of level and locality, in the course of cataloguing work.

those of the underlying beds except that some of them have well-developed lachrymal vacuities while others have none. Another new race also makes its appearance suddenly, and in great abundance, in the genus *Promerycochærus*—structurally derivable perhaps from some of the older oreodons, but not connected with them by intergradations. *Agriochærus* has disappeared. In the Upper Rosebud the *Oreodon-Merychys* phylum shows a distinct and marked advance in the length of the crowns of the teeth; lachrymal vacuities are always present, the feet are decidedly more compact and elongate. *Promerycochærus* disappears entirely and is replaced by a very distinct and more advanced genus *Merycochærus*. The *Leptauchenia* series has disappeared temporarily, to re-appear in the Middle Miocene in a more specialized genus, *Cyclopidius*, the last known member of this race.

The Middle Miocene (which should follow the Upper Rosebud) is unrepresented at the locality under consideration (Pine Ridge, South Dakota), but elsewhere overlies beds with an equivalent fauna, and contains *Merycochærus* in one locality with *Merychys* (both represented by more specialized species); in another locality it contains instead, *Promerycochærus* with *Ticholeptus* (allied to *Merychys*); in a third is found the most highly specialized member of the *Merycochærus* line, *Pronomotherium*. In the Upper Miocene and Lower Pliocene the oreodonts become much scarcer, and the skulls and skeletons are known only in two or three instances. *Pronomotherium* certainly occurs in Montana; in Nebraska the *Merychyi* are more advanced in dentition, belonging to a distinct subgenus *Metoreodon*; but whether the skulls and skeletons are equally different we do not yet know, nor are we in a position to say whether the change is gradual or saltatory.

But the sum of results in regard to the changes from one stage to another in this best known group of fossil mammals is either that the changes are abrupt, constituting clean-cut faunal divisions marked by the sudden appearance in abundance of a more advanced stage; or else that the new form replaces the older one little by little, but on the whole can not be fairly said to be gradually converted into it by infinitesimal gradations.

This general observation applies, in my opinion, equally well to any abundant group of fossil vertebrates whose phylogeny is sufficiently known to make them worth considering.

If, therefore, we consider that the record is continuous where there is no apparent stratigraphic break, and that the known record really represents what was going on over the entire continent of North America, I do not see that we can fairly escape from the conclusion that new species, new genera and even larger groups have appeared by saltatory evolution, not by continuous development.

But—and here lies the crux of the whole question—we have no

right whatsoever to make either of these assumptions. And without them the argument from paleontology for discontinuous development is almost or quite worthless.

If we consider the general conditions controlling evolution and migration among land mammals, it will be evident, I think, that—

1. The external conditions favoring the evolution and progress of a given phylum will not be uniformly developed all over the world or all over one continent, but will appear first, and be at all times more advanced, in some circumscribed region in one or another continent, or simultaneously in limited areas of two or more continents, similarly situated as to climate, temperature, etc.

2. The animal best able to take advantage of these conditions will be existing at the time (*a*) in one continent or (*b*) in more than one, or (*c*) different animals in different continents may be equally able to adapt themselves to the new conditions.

3. As a result, the new stages of any progressive race will first appear in a limited area and will spread out from that region as the favoring environment spreads, the race at the same time continuing its progress further within that area. This area will be the center of dispersal of the race. Its location will be conditioned by two factors, the early appearance of the new environmental conditions, and the existence of species most able to take advantage of these conditions. Parallelism and convergence in racial evolution will be conditioned by 2*b* and 2*c*.

4. Progressive change from uniformly warm to zonal climates during the Tertiary must needs have been a great factor in controlling the progress and distribution of Tertiary mammals. As the new conditions appeared first at the poles, the chief centers of dispersal of the animals adapted to them must have been in the northern parts of one or another of the great northern continents.² The exact location of the dispersal center for each race would be variously decided by the complex of environmental and faunal relations of each, and might be shifted from time to time by changes in these relations.

5. In the regions distant from the center of dispersal the geological record, if complete, should show the successive appearance of progressively higher types in a phylum, arriving in successive waves of migration, and each new type suddenly or gradually displacing the previous stages. Whether the evolution of a race at its center of diffusion was continuous or discontinuous, the geological record of its progress preserved in any other region would be apparently that of a discontinuous development. It would be not the actual history of its evolution but

² To a minor extent in the southern parts of the southern continents, whose restricted area and isolation prevailed in the writer's opinion throughout the Tertiary. There is some evidence, however, along the lines indicated in paragraphs 5 and 6, that Patagonia was the chief center of dispersal of South American Tertiary mammals.

an approximation to it. The closeness of the approximation would be largely measured by the nearness and accessibility of the region in question to the center of dispersal of the race.

6. If the evolution at the center of dispersal was sharply discontinuous this discontinuity would be merely emphasized elsewhere. If on the other hand it was continuous, we should get a near approach to continuity in a complete evolutionary series from a region not remote from the center of diffusion of the race, while the evolutionary series from the same region, of a race whose center of dispersal was remote, would be sharply discontinuous.

7. Applying these principles to some of our American Tertiary phyla, we find that certain phyla which we can be sure were of North American origin, such as the camels, oreodonts and peccaries, do present a much nearer approach to continuity of development than do other phyla which we can be sure were of old world origin, such as the deer, the antelopes or the proboscideans.

I assume that since the oreodonts and peccaries never reached the old world, and the camels did not reach it till the Pliocene, their centers of dispersal were well to the south of the Bering Sea connection with the old world. I assume that since the horses are represented by a double evolutionary series, one in Europe, a closer one in North America, their center of dispersal lay far enough north to spread into Europe on one hand, North America on the other, but that the latter was nearer or more accessible, *i. e.*, their center of dispersal was north-eastern Asia or Alaska. On similar grounds the center of dispersal of most of the Tertiary ruminants might be located in northwest Asia, of proboscideans in central Asia, of tapirs in northeastern Asia, of rhinoceroses northeast Asia and Alaska, of dogs in northwest Canada, and so on—a series of indefinite guesses which a careful study of the present geographic distribution, with these principles and the imperfect geologic data in mind, might serve to fix more definitely.

The point at present to be considered is that in such series as the camels, oreodonts and peccaries, we do have a sufficiently close approach to a continuous series to warrant our believing that the true process of their evolution in the center of their dispersal was a gradual one as regards the evolution of genera and higher groups, but for aught that paleontology tells to the contrary, it may have been partly, though not wholly, discontinuous and saltatory so far as the evolution of new species is concerned. But the larger and more complete the series of specimens studied, the more perfect the record in successive strata, and the nearer is the hypothetical center of dispersal of the race, the closer do we come to a phyletic series whose intergrading stages are well within the limits of observed individual variation in the race. The known facts in vertebrate paleontology are, in my opinion, utterly inadequate

to prove whether the development of races was or was not wholly continuous. But I think that the evidence, considered in relation to the imperfection of our knowledge, goes to show that the gaps were not normally wide. In exceptional cases I think we have reason to believe that they were wide (*Otocyon*, for instance), but in these instances the evidence is not that of the paleontological record.

